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A Theory of the Benham Top based on Center-Surround Interactions in the Parvocellular Pathway

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Abstract

A model color-opponent neuron was used to investigate the subjective colors evoked by the Benham Top (BT). Color-opponent inputs from cone-selective parvocellular (P) pathway neurons with center-surround receptive fields were subtracted with a short relative delay, yielding a small transient input in response to a white spot. This transient input was amplified by BT-like stimuli, modeled as a thin dark bar followed by full-field illumination. The narrow bar produced maximal activation of the P-pathway surrounds but only partial activation of the P-pathway centers. Due to saturation, subsequent removal of the bar had little effect on the P-pathway surrounds, whereas the transient input from the P-pathway centers was amplified via disinhibition. Responses to BT-like stimuli became weaker as surround sensitivity recovered, producing an effect analogous to the progression of perceived BT colors. Our results suggest that the BT-illusion arises because cone selective neurons convey information about both color and luminance contrast, allowing the two signals become confounded.

Introduction

The Benham Top (BT) was first described over a hundred years ago when it was reported that a spinning disc imprinted with a characteristic light and dark pattern elicited a perception of multi-colored rings (Benham, 1894). The most common version of the BT consists of two hemi-circles, one much darker than the other, with the lighter hemi-circle containing several thin, dark arc segments at various radii and azimuthal locations (fig. 1a). When this pattern is rotated at moderate velocities, on the order of 8 Hz (Jarvis, 1977), the concentric rings traced-out by the different arc segments appear colored (fig. 1b). The perceived colors produced by the individual arc segments, also called Benham-Fechner colors, pattern induced flicker colors (PIFCs) or subjective colors, are generally consistent across subjects and lie primarily in the blue/yellow plane (Schramme, 1992; von Campenhausen et al., 1992), indicating that red and green cones contribute equally to the phenomenon. The perception of colors is unchanged when a pair of identical BT stimuli are presented to both eyes simultaneously but at different relative phases, implying that the physiological mechanism, or mechanisms, responsible for the illusion are located prior to locus of binocular fusion (for a comprehensive review of BT phenomenology, see von Campenhausen and Schramme, 1995).

Several theories have been advanced to account for Benham-Fechner colors. It has been suggested that the BT-illusion could result from “rebound” responses in retinal ganglion cells (Grunfeld and Spitzer, 1995), but no such responses are elicited in primate midget or parasol ganglion cells by either small spots or annuli (Benardete and Kaplan, 1997). Other models of the BT-illusion have relied on differences in the temporal response properties of the three cone types (cf. Courtney and Buchsbaum, 1991).

However, timing differences alone cannot be the primary explanation. The perceived colors associated with the rings traced out by the inner- and outer-most arc segments are quite different, yet a plot of the incident light intensity vs. time would be indistinguishable for any arbitrarily chosen point beneath either of the two rings, except for a constant phase shift. Thus, any model of the BT illusion must account for spatial as well as temporal processing, particularly how responses to local changes in illumination are modulated by stimulation outside the receptive field center. Indeed, subjective colors disappear when BT-like stimuli are viewed through a pinhole so that only local intensity variations are visible (von Campenhausen and Schramme, 1995). Furthermore, any model of the BT illusion must contain an essential non-linearity. The component parts of the BT, such as the rotating arc segments or the alternating dark/light hemi-circles presented alone, do not elicit color percepts. The principle of linear superposition requires the existence of a non-linear mechanism to explain why the responses to the full BT-stimulus are qualitatively different from the sum of the responses to its component parts. Here, we describe a mathematical model of a cortical color-opponent neuron that reproduces key aspects of the BT illusion in a manner consistent with the anatomy and physiology of the primate color processing system. Before presenting the mathematical details of the model, however, we first provide a heuristic description of the key ideas.

Cortical color-opponent cells are thought to receive input from cone-selective P-pathway neurons possessing antagonistic center-surround receptive fields (fig. 2) (Derrington and Lennie, 1984; Livingstone and Hubel, 1984; Hubel and Livingstone, 1990; Croner and Kaplan, 1995; Benardete and Kaplan, 1997; Conway, 2001). Because the receptive fields of cortical color-opponent neurons are much larger than those of typical P-pathway retinal or LGN neurons (Conway, 2001), multiple red- and green-selective P-pathway cells will converge within the cortical neurons receptive field center, with the response polarity of the opponent input reversed in sign (fig 2b). P-pathway neurons have strong antagonistic surrounds (Croner and Kaplan, 1995; Benardete and Kaplan, 1997), which due to their small relative size and high convergence ratio, would overlap extensively within the cortical neuron's receptive field center (fig. 2c).

To further develop our heuristic model, we next consider the responses of a cortical color-opponent neuron to a BT-like stimulus. To simplify our description, the rotating BT is divided into three distinct phases (fig 3, top row): *Phase I*) no stimulus, *Phase II*) a stimulus consisting of a thin dark bar and *Phase III*) full-field stimulation. It is well established that the perception of subjective colors does not require motion *per se* and is readily elicited by the above sequence (von Campenhausen and Schramme, 1995). Our model depends on two critical assumptions. 1) The color-opponent inputs are slightly out of balance, so that there is a small residual transient even in response to a white spot that activates both cone types equally. Such an imbalance could arise from a short time delay between color-opponent inputs, but the precise mechanism is not critical to the present description. 2) Following the dark half-cycle, the P-pathway surrounds are effectively saturated by the brightly illuminated regions outside the dark, high-contrast bar and are therefore temporarily insensitive to further stimulation. Below, we outline how these two assumptions influence the responses of cortical color-opponent neuron to the three phases of stimulation making up a BT-like stimulus (fig. 3).

Phase I (fig. 3, left column): Because there is no stimulus, the cortical color-opponent neuron simply fires at a low background rate.

Phase II (fig. 3, middle column): In response to a thin dark bar positioned over the cortical neuron's receptive field, the P-pathway surrounds are activated maximally while the P-pathway centers are activated only partially, resulting in a net inhibitory input to the color-opponent neuron. This inhibition is masked, however, by the low background firing rate of the target cortical cell.

Phase III (fig. 3, middle column): With the onset of full-field stimulation, the P-pathway centers become strongly activated whereas the P-pathway surrounds, whose responses were previously saturated, are relatively unaffected. By eliminating the strong surround antagonism that is normally present, the residual color-opponent input to the cortical neuron is effectively unmasked. This enhancement, via disinhibition, is further illustrated by considering the responses of the same cortical neuron to a medium sized white spot in the absence of prior exposure to the thin dark bar (fig. 4). In this case, the residual transient due to the slight imbalance between color-opponent inputs is reduced by concomitant activation of the P-pathway surrounds. The above description thus provides a heuristic account for how a small imbalance between color-opponent inputs can be amplified by a BT-like stimulus.

A potential problem with the above heuristic model, however, is that the assumed imbalance in color-opponent inputs implies that a flashing white light, by itself, would appear colored. In the above example, the response of the cortical cell to a white spot yielded a small residual input from the activation of the P-pathway centers that was not entirely canceled by activation the P-pathway surrounds. It is possible that the transient responses resulting from a slight imbalance in color-opponent inputs could be suppressed by mechanisms higher up in the visual processing hierarchy or else their amplitude may be below the threshold for eliciting a color percept. Alternatively, the residual input from the color-opponent P-pathway could be canceled by an equal and opposite transient input from a separate processing stream, such as the luminance, or magnocellular (M) pathway (fig. 4). Because M-pathway receptive fields are larger than those in the P-pathway at corresponding eccentricities, their convergence ratio onto cortical color-opponent neurons would be correspondingly lower, resulting in much less overlap of the M-pathway surrounds within the cortical color-opponent neuron's receptive field center (fig. 2d). Disinhibition by a BT-like stimulus would therefore have much less effect on M-pathway vs. P-pathway inputs.

Although the above heuristic description is minimal in the sense that it includes only those elements deemed necessary to account for the BT illusion, it is nonetheless sufficiently complex that it is important to restate our hypothesis in terms of quantitative mathematical model. The development of an explicit model not only forces us to be concrete about our assumptions, but also allows us to make explicit comparisons with experimental data and to investigate the dependence on key parameters. Below, we present a quantitative mathematical model that accounts for the main aspects of the BT-illusion. As with our heuristic description, the mathematical model is minimal in the sense that it includes only those physiological and anatomical elements that are necessary to account for the target behavior. While the model could be made more biologically realistic, our goal in the present study was to identify a minimal set of assumptions sufficient to account for the BT-illusion. Before we turn to the mathematical formulation of the model, we list below, for completeness and ease of reference, the key assumptions upon which our theory of the BT-illusion is based.

Critical assumptions underlying the proposed model: 1) Cortical color-opponent cells possess a low background firing rate (Livingstone and Hubel, 1984; Hubel and Livingstone, 1990; Conway, 2001), causing them to be more sensitive to depolarizing than to hyperpolarizing inputs, 2) Color-opponent inputs to cortical cells arise from the P-pathway (Livingstone and Hubel, 1984; Hubel and Livingstone, 1990; Conway, 2001) and possess antagonistic center-surround receptive field components (Derrington and Lennie, 1984; Croner and Kaplan, 1995; Benardete and Kaplan, 1997), 3) P-pathway surrounds exhibit non-linear response saturation at high-contrast (Kaplan and Shapley, 1986) and 4) there is slight imbalance between color-opponent inputs, represented in our model by a short time delay.

Of the above postulated mechanisms, only the first two are directly supported by physiological data, while support for the third is indirect. Although the dynamics of response saturation in P-pathway surrounds has not, to our knowledge, been studied in primates, some inferences can be drawn from the response saturation of cat horizontal cells (Lankheet et al., 1993). Experimental support for the fourth of the above assumptions is presently lacking, but the sign inversion implicit in the subtraction of color-opponent inputs presumably requires an extra inhibitory interneuron and thus an additional synaptic delay. Finally, despite evidence for M pathway input to color processing regions (Ferrera et al., 1992; Lachica et al., 1992; Nealey and Maunsell, 1994; Edwards et al., 1995; Ding and Casagrande, 1998; Johnson et al., 2001), the assumption of a direct M-pathway input to cortical color-opponent neurons is highly speculative, and is best regarded as a mathematical convenience to ensure that the response to a flashing white spot is identically zero. Such a canceling mechanism is conservative from the point of view of our model, since it forces the responses to a BT-like stimulus to emerge from a flat baseline.

Methods

All input pathways were built from the same impulse kernel, from which the responses to arbitrary patterns of temporal modulation could be calculated by linear convolution. The impulse kernel consisted of two components, each constructed from cascaded low pass filters:

$$G(t) = A\left[\left(\frac{(t/\tau_1)^{n_1} e^{-t/\tau_1}}{n_1!}\right) - R\left(\frac{(t/\tau_2)^{n_2} e^{-t/\tau_2}}{n_2!}\right)\right] \tag{1}$$

with τ_1, τ_2 = 2 msec, $n_1 = 1$, $n_2 = 7$, $R = 0.75$, and A an arbitrary normalization factor determined numerically so that the sustained response to a unit input was equal to one. The above parameters provided a good fit to the time course of the impulse kernels recorded from the responses of P ganglion cells to center and surround stimulation (Benardete and Kaplan, 1997), except for a fixed onset latency, which is not modeled by the above expression. The above impulse kernel, $G(t)$, was used to calculate the total input to the cortical neuron from the red-selective P pathway centers, denoted by $P_{\text{Red,Center}}$, via linear convolution:

$$P_{\text{Red,Center}}(t) = G(t) * \left[S_{\text{Red,Center}}\right]_{\text{Max=1}}, \tag{2}$$

where $S_{\text{Red,Center}}$ ($S_{\text{Green,Center}}$) represents the time-dependent activation of red (green) cones within the cortical neuron’s receptive field center and the notation $[]_{\text{Max=1}}$ stipulates that the quantity inside the brackets saturates at a value equal to one (i.e. $[x]_{\text{Max=1}} = x$, $x \leq 1$,

$[x]_{\text{Max=1}} = 1$, $x > 1$). For simplicity, we have lumped all of the non-linear saturation in the model into the input stage, but in principle this saturation could distributed more realistically along the color processing stream.

The input to the model cortical neuron from the red-selective P pathway surrounds, $P_{\text{Red,Surround}}$, was computed as:

$$P_{\text{Red,Surround}}(t) = \frac{1}{2} \cdot \begin{pmatrix} G(t) * \left[0.5 \cdot S_{\text{Red,Center}} + S_{\text{Red,Surround}}\right]_{\text{Max=1}} \\ + G(t) * \left[0.5 \cdot S_{\text{Green,Center}} + S_{\text{Green,Surround}}\right]_{\text{Max=1}} \end{pmatrix}. \tag{3}$$

where $S_{\text{Red,Surround}}$ ($S_{\text{Green,Surround}}$) denotes the time-dependent activation of red (green) cones within the annulus corresponding to the exclusive portion of the cortical neuron's receptive field surround (the portion of the surround exclusive of the receptive field center). Due to the assumed high spatial convergence of P pathway inputs to the model cortical neuron, stimulation of the cortical neuron's receptive field center was assumed to produce a relatively large activation of the P pathway surrounds, with the maximum activation (due to center stimulation) being set to 0.5, thus accounting for the dependence of $P_{\text{Red,Surround}}$ on $S_{\text{Red,Center}}$ and $S_{\text{Green,Center}}$. The chromatic sensitivity of the P pathway surrounds was assumed to be broadband, having equal contributions from red and green selective channels regardless of the spectral selectivity of the receptive field center. For simulating the responses to black and white stimuli, such as the BT, the spectral composition of the red and green surrounds was not of fundamental importance, as this aspect of the model only affected the activity evoked by colored stimuli. For simplicity, we did not include delays in the activation of the antagonistic surround, which would have complicated the model by introducing additional time constants but would not have affected our main conclusions. The total input to the cortical neuron from the red-selective component of the P pathway, P_{Red}, was then given by:

$$P_{\text{Red}}(t) = P_{\text{Red,Center}}(t) - P_{\text{Red,Surround}}(t)\,. \tag{4}$$

For the chromatically opponent green-selective input channel, we used the same impulse kernels as for the red channel with the addition of a small delay,

$$\begin{aligned} P_{\text{Green}}(t) &= \left\lfloor P_{\text{Green,Center}} - P_{\text{Green, surround}} \right\rfloor \\ &= G(t-t_d) * \left[S_{\text{Green,Center}} \right]_{\text{Max=1}} \\ &\quad - \frac{1}{2}\begin{pmatrix} G(t-t_d) * \left[0.5 \cdot S_{\text{Green,Center}} + S_{\text{Green,Surround}}\right]_{\text{Max=1}} \\ + G(t-t_d) * \left[0.5 \cdot S_{\text{Red,Center}} + S_{\text{Red,Surround}}\right]_{\text{Max=1}} \end{pmatrix}, \end{aligned} \tag{5}$$

where $t_d = 7$ msec.

The total input from the P pathway to the red-green opponent cortical neuron was simply the sum of the individual inputs from the red- and green-selective components:

$$P(t) = \left[P_{\text{Red}}(t) - P_{\text{Green}}(t) \right]. \tag{6}$$

With a trivial exchange of labels, the same model could equally well describe a green-red opponent cortical neuron, and all of the following results would apply. Because the BT activates both red and green channels with equal strength (Schramme, 1992), the implied symmetry between red- and green-selective cortical neurons was essential.

The luminance or M pathway responded transiently to white light and was achromatic, receiving equal red and green inputs:

$$\begin{aligned} M(t) &= \left[M_{\text{Center}} - M_{\text{Surround}}\right] \\ &= \frac{1}{2}\cdot\left(\begin{array}{l} G(t)*\left[0.5\cdot S_{\text{Red,Center}} + 0.5\cdot S_{\text{Green,Center}}\right]_{\text{Max=1}} \\ -G(t-t_d)*\left[0.5\cdot S_{\text{Red,Center}} + 0.5\cdot S_{\text{Green,Center}}\right]_{\text{Max=1}} \end{array}\right) \\ &\quad -\frac{1}{2}\cdot\left(\begin{array}{l} G(t)*\left[0.5\cdot S_{\text{Red,Surround}} + 0.5\cdot S_{\text{Green,Surround}}\right]_{\text{Max=1}} \\ -G(t-t_d)*\left[0.5\cdot S_{\text{Red,Surround}} + 0.5\cdot S_{\text{Green,Surround}}\right]_{\text{Max=1}} \end{array}\right). \end{aligned} \tag{7}$$

The main difference between the luminance and chromatic pathways was that the surround component of the luminance pathway did not overlap with the cortical neuron’s receptive field center and thus was not activated by a “small” spot. We could have allowed the M pathway surrounds to partially overlap the cortical neuron’s receptive field center without modifying our basic conclusions, as long as the overlap of the P pathway surrounds remained much greater, but we opted instead for the simplest implementation. To balance the M and P pathway inputs, the input from the luminance pathway to the cortical opponent neuron was reduced by 50% relative to that of the chromatically opponent pathway. This accounted for the fact that the net P pathway input to the cortical opponent neuron was itself reduced by 50% due to the extensive overlap of the P pathway centers and surrounds.

The model employed no explicit spatial convolutions. Instead, we considered only a few stimulus classes (small spots, annuli, and full field stimulation) for which the relative activation of the different receptive field components could be reasonably specified 'by hand'. For a small white spot, we used $S_{\mathrm{Red,Center}} = S_{\mathrm{Green,Center}} = 0.5$, $S_{\mathrm{Red,Surround}} = S_{\mathrm{Green,Surround}} = 0$, while for a small red spot, we used $S_{\mathrm{Red,Center}} = 0.5$, $S_{\mathrm{Green,Center}} = 0.25$, $S_{\mathrm{Red,Surround}} = S_{\mathrm{Green,Surround}} = 0$. For a full-field white spot, the activation of all receptive field components was the same, so that $S_{\mathrm{Red,Center}} = S_{\mathrm{Green,Center}} = S_{\mathrm{Red,Surround}} = S_{\mathrm{Green,Surround}} = 1$. For a high contrast dark narrow bar, we set $S_{\mathrm{Red,Center}}=S_{\mathrm{Green,Center}}=0.5$ and $S_{\mathrm{Red,Surround}}=S_{\mathrm{Green,Surround}}=1$.

When an input pathway was saturated, its sensitivity recovered with a time constant of 50 msec. Thus, if a thin dark bar was presented for a period much greater than 50 msec, the modulation in the surround input at bar offset became exactly as predicted by the linear model (i.e. the Max=1 condition was ignored). For intermediate durations, the modulation in the surround input due to the offset of a dark bar was interpolated between these two extremes, exponentially approaching that of the linear model with a time constant of 50 msec. It was not necessary to model the recovery of sensitivity in order to unmask responses to BT-like stimuli, but such recovery was essential to account for the absence of responses to a flashing dark spot. In addition, the recovery of sensitivity caused the responses to a BT-like stimulus to depend on the delay between the onset of the light half-cycle and onset of the dark, narrow bar, thereby providing a possible account for the different subjective colors elicited by arc segments with different onset delays.

Finally, the responses of the cortical neuron to positive and negative inputs was assumed to be asymmetric, produced by a sigmoidal input/output function of the following form:

$$R = \frac{1}{1 + e^{-4\alpha(I-\theta)}} \,. \tag{8}$$

where R is the output response, normalized between zero and one, I is the input, given by P–M, and the gain, α, and the threshold, θ, were set to 3.75 and 0.15, respectively. Such rectification, possibly representing a positive threshold for spike generation, was not necessary to produce temporally modulated input to BT-like stimuli, but was necessary to unmask a net positive response.

Equations 1-8 represent a minimal model of a cortical opponent neuron that did not respond to either small or large flashing white or black spots, but did respond to red spots and to BT-like stimuli. A schematic of the model is shown in figure 5.

Results

A small flashing white spot, which remained on for half a cycle, equal to 128 msec out of a total cycle length of 256 msec, did not activate the model cortical color-opponent neuron (fig. $6a_1$). Due to the slight imbalance in color-opponent inputs, the small white spot produced a small positive transient input from the red–green centers (fig. $6c_1$) and a smaller negative transient input from the red–green surrounds (fig. $6d_1$), yielding a net positive input from the color-opponent pathway (figs. $3b_1$, dashed line). The same small flashing white spot produced a small negative transient input from the luminance pathway (figs. $3b_1$, dotted line) that was equal and opposite to the transient input from the P-pathway, resulting in no net input to the model cortical cell (fig. $3b_1$, solid line).

A large flashing white spot also produced no net response in the cortical neuron (fig. $6a_2$), although in this case the net inputs from the color-opponent and luminance pathways were both zero (fig. $6b_2$). For a large white spot, the input from the P pathway surrounds (fig. $6d_2$) exactly cancelled the input from the P pathway centers (fig. $6c_2$) and similarly for the luminance pathway. The above results illustrate how spatially and chromatically opponent inputs were combined so as to ensure that a flashing white spot produced no net response in the model cortical neuron.

The model cortical neuron generated sustained positive responses to a small red spot flashed at the same temporal frequency (fig. $7a_1$). A red light activated the green opponent channel at reduced strength, here taken to be 50% of that elicited by a white spot, yielding a sustained positive input from the red–green centers (fig. $7c_1$). There was also a sustained input from the red–green surrounds of opposite sign (fig. $7d_1$), but this was not as large as the input from the red-green centers due to the small spot size used. A small red spot thus resulted in a net sustained input from the color-opponent pathway (fig. 7b$_1$, dashed line) whereas the luminance channel was only transiently activated (fig. 7b$_1$, dotted line). Recall that in the present model, M-pathway inputs were always transient by explicit construction.

A large red spot evoked an even bigger response from the model cortical cell (figs. 7a$_2$), due to the increased activation of the red–green centers (fig. 7c$_2$), whereas the achromatic red and green P pathway surrounds exactly cancelled except for a short transient (fig. 7d$_2$). This cancellation of surrounds in the red–green pathway depended on the assumption of broadband spectral sensitivity. Large red spots would have elicited different responses if the red and green surrounds had possessed different spectral sensitivity, but this aspect of the model was not critical for analyzing responses to black and white stimuli, which was our primary interest here. The absence of strong surround activation led to a large net input from the color-opponent pathway (fig. 7b$_2$, dashed line), whereas there was no input at all from the luminance pathway (fig. 7b$_2$, dotted line), whose center and surround components cancelled identically. The model cortical neuron thus exhibited color selectivity, generating sustained positive responses to flashing red spots but not to white spots.

To mimic a BT-like stimulus, we adopted the following protocol, which was similar to that illustrated in figure 3. One cycle of the BT-like stimulus lasted 256 msec, corresponding to a rotation rate of approximately 4 Hz. Each cycle was divided into equal light and dark half-cycles representing the passage of the black and white hemicircles comprising the standard top. A narrow, dark bar was used to represent the passage of a thin arc segment through the receptive field center of the cortical neuron, covering ½ of the cortical neuron's receptive field center. After 32 msec following the onset of the light half-cycle, corresponding to 1/8th of the total cycle, the dark bar was removed, resulting in full-field uniform stimulation. The dark bar itself produced maximal activation of the red and green surrounds (fig. $8d_1$) but only partial activation of the red and green centers (fig. $8c_1$), resulting in a net negative input from the red–green pathway during phase II of the cycle (fig. $8b_1$, dashed line). Subsequent removal of the dark bar produced an opposite effect: greater activation of the red and green centers than of the red and green surrounds, yielding a net positive input (fig. $8b_1$, dashed line).

Removal of the dark bar had relatively little effect on the total activation of the red and green surrounds because these were already saturated. The arrow in figure $8d_1$ points to the absence of any noticeable modulation in the input from the P-pathway surrounds. Thus, upon removal of the dark bar, the input from the uncovered red and green centers was unopposed by an antagonistic response peak from the red and green surrounds, resulting in a net positive input from the P-pathway (fig. $8b_1$, dashed line). Importantly, there was no countervailing amplification of the net input from the luminance pathway (fig. $8b_1$, dotted line), whose centers and surrounds were non-overlapping, resulting in a net positive input to the cortical cell during phase II (fig. $8b_1$, solid line). Due to the asymmetry in the input/output properties of the model cortical neuron, the overall response to the BT-like stimulus was positive (fig. $8a_1$).

A purely linear model that lacked input saturation did not respond to a BT-like stimulus (fig. $8a_2$), as the input from the red–green pathway (fig. $8b_2$, dashed line) was reduced by surround antagonism so that it became equal and opposite to the input from the luminance pathway (fig. 8b$_2$, dotted line). To allow direct comparison with the nonlinear model, the linear model was calibrated to produce identical responses to flashing small and large white spots. The input from the P pathway centers was unaffected by linearization (compare fig. 8c$_2$ with fig. 8c$_1$) as was the input from the luminance pathway (compare fig. 8b$_2$ with fig. 8b$_1$, dotted lines). The P pathway surrounds, however, were less strongly activated by the annulus onset and more strongly modulated by the annulus offset after linearization (compare fig. 8d$_2$ with fig. 8d$_1$, arrows).

To illustrate the critical role played by differences in the spatial convergence of the two input pathways, the red and green surrounds were instead modeled as non-overlapping, thus making the spatial organization of the red-green opponent pathway identical to that of the luminance pathway. The overall input to the luminance pathway was doubled to compensate for the fact that the red and green centers were no longer antagonized by spatially overlapping surrounds. In this situation, the model cortical cell no longer responded to the BT-like stimulus (fig. 8a$_3$). Indeed, with identical spatial organizations, the input from the red–green pathway (fig. 8b$_3$, dashed line) became indistinguishable, except for a change in sign, from that of the luminance pathway (fig. 8b$_3$, dotted line). These controls show that the model's responses to the BT-like stimulus depended on two critical elements: 1) saturation of the red and green surrounds by a high contrast annulus and 2) the high spatial convergence of the P-pathway.

The model also suggested a physiological correlate of the different colors produced by the BT stimulus. Arc segments connected to the trailing edge of the dark hemi-circle appear reddish-brown while those attached to the leading edge appear dark blue or violet (Schramme, 1992). We hypothesize that such differences in perceived color will be reflected in the degree to which red- and green-selective cortical opponent neurons were activated by the different arc segments, thus shifting the perceived color within the blue-yellow plane. To test this hypothesis, the model cortical neuron was driven by a BT-like stimulus in which the delays between the onset of the light half-cycle and that of the dark bar were adjusted so as to represent arc segments at different azimuthal locations relative to the trailing edge of the dark hemi-circle (fig 9a). As a function of increasing delay, the net response to the BT-like stimulus progressively declined. The red and green surrounds were immediately saturated upon onset of the light half-cycle, but the surround sensitivity then recovered with a time constant of 50 msec. The longer the delay, the more linear the red and green surrounds became and thus more sensitive to the introduction and removal of the dark bar. This linearization, in turn, systematically reduced responses to BT-like stimuli at increasing delay. Moreover, the persistence of responses at lower levels of surround saturation shows that maximal saturation was not necessary for the current model. It is clear that at effectively infinite delays, the sensitivity of the red and green surrounds would fully recover, thus accounting for the absence of a response in the cortical color-opponent neuron to a flashing dark spot on a light background. The model therefore predicts there would be no activation of a red- or green-selective color-opponent cortical neuron produced by the rotating arc segments alone. Rather, the recovery of the surround sensitivity following saturation by a high-contrast annulus predicts that only the full BT-like stimulus will produce a color percept.

We also examined the consequences of varying the effective rotation speed of the BT-like stimulus (fig. 9b). Measured as the total integrated output of the cortical neuron over a fixed duration equal to 1 sec, responses to the BT-like stimulus were band-passed, peaking around 8 Hz and falling off at both lower and higher frequencies. Starting at zero, the initial increase in integrated response with rotation frequency could be attributed to two factors: 1) the extra number of cycles within the fixed integration period, with each cycle producing an approximately equal contribution, and 2) the tendency for surround sensitivity to recover over the duration of a single annulus presentation for very slow rotation speeds. For rotation frequencies above 8 Hz, the decline in the integrated response amplitude follows from the kinetics of the response kernel and from the low-pass filtering introduced at the input stage of the model. At a rotation frequency of 32 Hz, for example, each arc segment lasts for only 4 msec, which was too short for the peak of the P pathway surround response to substantially decay before the onset of full-field stimulation. Additional stages of low pass filtering could, in principle, be incorporated into the model to produce a more realistic frequency dependence.

To better illustrate the dynamics of saturation and recovery employed in the model, we consider in greater detail the modulation of the surround input produced by the introduction and removal of the dark bar as a function of the total cycle duration (fig 10). At long durations (0.5 Hz), the recovery from saturation is more-or-less complete and the surround input can be strongly modulated by a dark, narrow bar. Moreover, the later in the light half-cycle the dark bar is introduced, the stronger the resulting modulation. On the other hand, for relatively short cycle durations (4 Hz), the sensitivity of the surround pathway has little time to recover and the introduction and removal of the dark bar has only negligible effect on the total input.

It has been shown that subjective colors can still be elicited by BT-like stimuli in which the sharp spatial boundaries characteristic of the standard pattern are replaced by smooth graduations (Tritsch, 1992). Specifically, the square-wave light-dark cycle can be replace by a sinusoidal modulation at the same fundamental frequency. Likewise, the individual arc segments can be replaced by patches with smoothly varying boundaries. Our model cortical color-opponent cell similarly exhibits responses to a BT-like stimulus in which the sharp boundaries between stimulus phases have been replaced by smooth temporal variations (fig. 11a_1-e_1). As in the above cited experiments, the light and dark half-cycles were replaced by a pure sinusoidal variation and the sharp onsets and offsets of the dark bar were replace by a Gaussian modulation with an equivalent mean duration (fig. 11e_1). We have further verified that smoother Gaussian profiles, corresponding to longer mean durations, produced qualitatively similar results (not shown). Thus, the proposed model is consistent with the ability of BT-like stimuli that lack sharp contrast boundaries to nonetheless evoke subjective colors.

Finally, we demonstrate that the present results did not depend qualitatively on the precise values of key temporal parameters in the model (fig. 12). Specifically, the time delay between color-opponent inputs was varied by approximately ±25% without fundamentally altering the main characteristics of the frequency response curve. However, lengthening this delay, by increasing the relative imbalance between the color-opponent inputs, did increase the overall magnitude of the responses to BT-like stimuli, and likewise for smaller delays. Similarly, the adaptation time constant governing the recovery from saturation could be changed by ±50% without changing the qualitative character of our results. Thus, we are confident that the present model is robust with respect to variations in key parameter values.

Discussion

We have presented a theory of the Benham Top (BT) illusion based on the responses of a model cortical neuron configured to respond selectively to red, but not to white or black, spots. Our model was intentionally restricted to a minimum number of physiological and anatomical elements necessary and sufficient to account for the phenomenon. Thus, certain well-known features of visual processing, such as the delay between center and surround activation, were not included in the model since such delays were not directly relevant to our hypothesis. On the other hand, the model incorporated several assumptions for which there is varying degrees of experimental support.

Color-selective neurons in the primary visual cortex that receive input from both red and green cones and are chromatically opponent have been previously described (Hubel and Livingstone, 1990; Conway, 2001), consistent with the main features of the model cortical neuron employed here. Color-opponent neurons in the primary visual cortex are thought to receive chromatically selective input from the P pathway (Hubel and Livingstone, 1990; Conway, 2001), but there is evidence for M pathway input to color processing circuits as well (Ferrera et al., 1992; Lachica et al., 1992; Nealey and Maunsell, 1994; Edwards et al., 1995; Ding and Casagrande, 1998; Johnson et al., 2001). Cells in both the P and M pathways have center-surround receptive field organizations with M pathway receptive fields being several times larger at any given eccentricity (Derrington and Lennie, 1984; Croner and Kaplan, 1995). Thus, the inputs to the model cortical neuron possessed a spatial organization and spatial convergence that was consistent with the known anatomy and physiology of the M and P pathways, although the existence of a direct input to color-opponent cells from the luminance channel is still rather speculative. However, our main finding--that small imbalances in color-opponent inputs can be amplified by BT-like stimuli--does not depend on the existence of a direct M-pathway input to the color-processing stream. Rather, transient input from the luminance pathway was employed as a mathematically convenient mechanism to cancel the transient input from the color-opponent pathway evoked by achromatic stimuli. Also consistent with the present model, the M pathway is generally characterized by more transient responses compared to the P pathway (Derrington and Lennie, 1984; Hubel and Livingstone, 1990). While the model assumed that M-pathway inputs consisted of purely transient responses, a small tonic component could have been added to the luminance pathway without fundamentally altering our conclusions if balanced by a similar sustained component from the color-opponent pathway. Indeed, the additional imbalance between color-opponent inputs implied by a net tonic component in the P-pathway would only amplify the effects reported here.

There is currently insufficient data to determine whether opponent inputs to color-selective cortical neurons are transiently activated by small white spots. However, such a possibility is not unreasonable. In the red-green opponent pathway, for example, the antagonistic green input might arise from an ON-green P-pathway LGN cell whose output is inverted by a cortical interneuron, thus introducing a small delay of a magnitude consistent with that assumed in the model (7 msec). Alternatively, the antagonistic green input might arise from an OFF cell that produced a reduction in tonic excitation at light onset. Since the level of excitation cannot drop below zero, bright stimuli might clip the signals from an OFF input during the response peak, thereby uncovering a small transient from the color-opponent ON input.

The responses of P pathway cells saturate at high contrast, while those of M pathway cells saturate at lower contrast (Kaplan and Shapley, 1986). The model required that a high-contrast annulus saturate the responses of the red and green P pathway surrounds. A fundamental prediction of the model therefore is that the BT phenomenon should disappear at low contrast, to which P pathway surrounds respond linearly. Furthermore, the model required that the saturation of the red and green surrounds by a dark narrow bar be temporary, and that adaptation mechanisms acting over tens to hundreds of msec restore the linearity of responses to subsequent modulation. Adaptation mechanisms such as these have been reported (Yeh et al., 1996).

The model can qualitatively account for additional aspects of the BT phenomenon beyond those already described. When the arc segments making up a BT stimulus are very wide, they trace out thick rings that only appear colored along their inner and outer edges while the central portion appears gray (von Campenhausen and Schramme, 1995). In our model, a thick dark bar, corresponding to a thick arc segment, would no longer saturate the red and green surrounds and thus would not be predicted to evoke a color percept expect near the edges, where surrounds would be strongly activated. The BT-illusion also goes away when the rotating pattern is viewed through a pinhole such that only a small part of the pattern is visible (von Campenhausen and Schramme, 1995). Again, this can be accounted for in the present model as resulting from a lack of saturation of the red and green surrounds as the outer radius of the annulus surrounding the dark bar is collapsed inward. The model is also consistent with selective cone demodulation experiments showing that the BT phenomenon requires activation of either red or green photoreceptors, but not blue photoreceptors (von Campenhausen et al., 1992). Clearly, the model of a red-green (or green-red) color-opponent cortical neuron presented here would not respond at all if both middle and long wavelength cones were demodulated simultaneously. There is, however, evidence that short wavelength cones also provide input to cortical red-green opponent neurons (Conway, 2001) as well as to cells in the M pathway (Chatterjee and Callaway, 2002). Although the possible contribution from blue cones was not addressed in the present model, the inclusion of such input should not fundamentally affect our main conclusions because blue-yellow cells in the K pathway do not respond to white light (de Monasterio, 1978; Zrenner and Gouras, 1981). The present model does not account for the subjective colors produced by temporal contrast modulation alone (Festinger et al., 1971), reports of which have been challenged (Jarvis, 1993).

While other quantitative models of the BT phenomenon have been proposed (Courtney and Buchsbaum, 1991; Grunfeld and Spitzer, 1995), the present model is unique in the following respects: 1) the model assumes no fundamental difference in the dynamics of the red and green pathways, except for a small fixed time delay and/or a purely ON/OFF asymmetry, 2) the model employs a linear impulse kernel consistent with the measured phasic-tonic responses of P ganglion cells, and 3) the model utilizes differences in the spatial convergence of the P vs. M pathways. Interestingly, the model implies that the BT phenomenon exists only because color-selective cells in the P pathway possess antagonistic surrounds and that subjective colors would not be produced if red- and green-selective neurons instead had receptive field structures like those of blue-yellow ganglion cells, which lack conventional surrounds (de Monasterio, 1978; Zrenner and Gouras, 1981). From this perspective, the BT-illusion is an artifact of using a single visual pathway, the P pathway, to convey information about both chromatic and luminance contrast (Hubel and Livingstone, 1990). Since the P pathway is thought to underlie high spatial acuity, or form, vision (Merigan et al., 1991), antagonistic surrounds are necessary to ensure the transmission of local contrast, as opposed to simple luminance. Such multiplexing of chromatic and luminance contrast, while efficient, perhaps makes the mammalian color-processing system susceptible to being spuriously activated by cleverly arranged black and white stimuli. Given the simplicity of the present model, and its strong connection to known physiology and anatomy, we hope that it may provide motivation for future experimental studies of the Benham Top.

Figure Captions

Fig. 1. Example Benham Top (BT). a) Stationary black and white pattern. The BT typically consists of a dark hemi-circle opposite to several short arc segments located at different angular and radial distances. b) Perceived colors. When rotated at angular velocities around 8 Hz, the concentric rings traced out by the different arc segments appear colored. The colors shown are illustrative only and do not attempt to accurately reproduce perceived colors.

Fig. 2. Receptive field structure of a model cortical color-opponent cell receiving convergent input from both P and M pathways. a) Structure of the color-opponent or P pathway input. The model cortical cell received color-opponent input from red- and green-selective channels of opposite polarity. b) High spatial convergence of P pathway receptive field centers. Input from P pathway centers was restricted to the cortical neuron’s receptive field center. Mathematically, such inputs were treated as pooled quantities. c) Antagonistic surrounds in the P pathway overlapped extensively. Stimulation of the cortical neuron’s receptive field center activated both center and surround components in the P pathway. d) Structure of the luminance or M pathway input. Unlike the color-opponent pathway, the center and surround components of the luminance pathway were spatially segregated.

Fig. 3. Heuristic model of the responses of a color-opponent neuron to a BT-like stimulus. Top Panel: Stimulus protocol. A BT-like stimulus is constructed from three

distinct phases. Phase I (left column): No stimulus. Phase II (middle column): A dark, narrow, high-contrast bar. Phase II (right column): Full-field stimulation. 1st row: Output of the color-opponent cell. In the absence of stimulation (phase I), the background firing rate is low, masking the effects of inhibitory input (phase II). The onset of full-field stimulation (phase III) produces a burst of spikes in the color-opponent neuron. 2nd row: Input to the color-opponent cell. Onset of the dark bar (phase II) produces a net inhibitory input, whereas removal of the dark bar (phase III) produces a net excitatory input. 3rd row: Input to the color-opponent cells from the pooled P-pathway centers. Due to a small imbalance in color-opponent inputs, there is a transient excitation from the P-pathway centers at both the onset (phase II) and offset (phase III) of the dark bar. 4th row: Input to the color-opponent cell from the pooled P-pathway surrounds. The bright regions surrounding the dark, narrow bar saturate the pooled P-pathway surrounds (phase II), so that there is no corresponding activation at bar offset (phase III). For simplicity, the contribution from the luminance pathway was omitted from this example.

Fig. 4. Heuristic model of the responses of a color-opponent neuron to a flashing white spot. Same organization as figure 3. Top panel: Stimulus protocol. Phases I & II: No stimulation. Phase III: A small white spot. 1st row: Output. The color-opponent cell does not respond to the white spot. 2nd row: Input. There is no net input to the color opponent cell (solid line) because the transient input from the P-pathway (dashed line) is cancelled by an equal and opposite input from the M-pathway (dotted line). 3rd row: P-centers. Due to a small imbalance between the color-opponent inputs, the white spot (phase III)

evokes a transient excitatory input from the P-pathway centers. 4th row: P-surrounds. Due to the imbalance between color-opponent inputs, the white spot (phase III) also produces a transient inhibitory input from the P-pathway surrounds, which is reduced in magnitude as a result of the small spot size.

Fig. 5. Schematic diagram of the mathematical model of a cortical color-opponent neuron. The stimulus is divided into center and surround components. Each input component passes through spectral filter (either red, green or gray) and is subjected to a saturation condition (maximum output equals one). Following saturation, sensitivity recovers with an exponential time constant of 50 msec, implemented by interpolating between the fully saturated and unsaturated states. Each input component is low pass filtered (time constant, 20 msec) and convolved with a response kernel matched to the measured kinetics of primate midget ganglion cells. Inputs along the green pathway are delayed by 7 msec. The response kernel along the luminance pathway is the difference in the response kernels along the red and green pathways and is therefore inherently transient. The different receptive field components are summed, with appropriate signs, into the color-opponent cell and the output filtered by a sigmoidal non-linearity.

Fig. 6. Responses of the model color-opponent neuron to flashing white spots. Top illustration: The stimulus was either a small (left column) or large (right column) flashing white spot. a_1) Output of the model color-opponent neuron. The small flashing white spot produces no net response. b_1) Input to the model color-opponent neuron. Transient input from the red–green pathway (dashed line) was exactly cancelled by an equal and

opposite input from the luminance pathway (dotted line), resulting in no net input to the color-opponent cell (solid line). c_1) Input to the color-opponent neuron from the pooled P-pathway centers. Due to the delay between the red and green pathways, the white spot elicits a transient excitation from the P-pathway centers. d_1) Input to the color-opponent neuron from the pooled P-pathway surrounds. Again due to the delay between the red and green pathway, there is a transient inhibition from the P-pathway surrounds which, due to the small spot size, is smaller than the corresponding excitation from the P-pathway centers. e_1) Stimulus protocol. The spot was turned on for one half, or 128 msec, of each stimulus cycle. Height of the stimulus trace was proportional to the total illumination of the color-opponent neuron's receptive field center. a_2-e_2) Same organization as a_1-e_1, with the small spot replaced by a large spot. a_2) Output. The large white spot evokes no response. b_2) Input. The net input along both the P- and M-pathways is zero due to exact center-surround cancellation. c_2) P-centers. Input from the P-pathway centers is larger than that evoked by a small spot due to the greater portion of the color-opponent neuron's receptive field activated. d_2) P-surrounds. Input from the P-pathway surrounds is increased by an even greater fraction by the larger spot size. e_2) Stimulus protocol identical to small spot. Vertical scale bars are always 0.5 in normalized dimensionless units.

Fig. 7. Responses of the model color-opponent neuron to flashing red spots. Same organization as figure 6. Top illustration: The stimulus was either a small (left column) or large (right column) flashing red spot. a_1) Output. The small flashing red spot produced a large sustained response. b_1) Input. Sustained input from the red–green

pathway (dashed line) was only weakly opposed by transient inhibition from the luminance pathway (dotted line), resulting in a large sustained net input to the color-opponent cell (solid line). c_1) P-pathway centers. The opponent green channel was only partially activated by the red spot, leaving a sustained input from the red–green centers. d_1) P-pathway surrounds. The spectrally broad-band red–green surrounds were only transiently activated. e_1) Stimulus protocol. a_2-e_2) Same organization as a_1-e_1, with the small spot replaced by a large spot. The interpretation of all panels is the same, except that the larger spot, by activating a greater portion of the receptive field, elicits a stronger input from the P-pathway and no net input from the M-pathway due to center-surround cancellation.

Fig. 8. Responses of the model color-opponent neuron to a BT-like stimulus. Top illustration: A BT-like stimulus was constructed from three sequential stimulus phases: Phase I (left): no stimulation, Phase II (middle): a narrow, high-contrast dark bar aligned with the receptive field center, Phase III (right): large white spot. *Left column*: Responses of the standard model. a_1) Output. The model color-opponent neuron exhibits a net positive response to the BT-like stimulus. b_1) Input. An inhibitory input from the red–green pathway was evoked at bar onset and an excitatory input at bar offset (dashed line). The antagonistic input from the luminance pathway was smaller (dotted line), resulting in a net input to the color-opponent cell (solid line). c_1) P-pathway centers. Due to the small delay between color-opponent inputs, a transient excitation from the red-green pathway was evoked at both bar onset and bar offset. d_1) P-pathway surrounds. Due to non-linear saturation of the P-pathway surrounds at bar onset, bar offset did not

evoke an appreciable response. e_1) Stimulus protocol. The intermediate trace height corresponds to the dark, high-contrast bar. a_2-e_2) Responses of the linearized model. Same organization as a_1-e_1. Without saturation, reduced red-green surround activation at bar onset (panel d_2) and increased activation at bar offset (panel d_2, arrow), reduced the total P pathway input (panel b_2, dashed line) so that it was equal and opposite to the M pathway input (panel b_2, dotted line), resulting in no net input to the color-opponent cell (panel b_2, solid line). a_2-e_2) Responses of the non-overlapping centers and surrounds model. Same organization as a_1-e_1. With identical receptive field organizations, input from the P- and M-pathways were necessarily equal and opposite despite saturation.

Fig. 9. Responses of the model color-opponent cell to a BT-like stimulus rotated at different speeds. a) Responses of the model color-opponent neuron to BT-like stimuli for different delays of the bar onset relative to the beginning of the light half-cycle. Red trace: Delay = 0. Yellow trace: delay = 1/8th cycle (32 msec). Green trace: delay = 1/4th cycle (64 msec). Blue trace: delay = 3/8th cycle (96 msec). The magnitude of the response decreased with increasing delay. b) Integrated response of the model color-opponent cell to BT-like stimuli as a function of temporal frequency. Different traces correspond to different delays, measured as a fraction of the total cycle length, as described in panel a. The integrated response peaked at around 8 Hz.

Fig. 10. Dynamics of input saturation and recovery of sensitivity. Total input to the P-pathway surrounds in response to a BT-like stimulus is plotted for a range of frequencies and onset delays. Left column: Onset delay = 0. Right column: Onset delay = ¼ cycle.

At a low cycle frequency (0.5 Hz, 1st row), sensitivity recovers sufficiently from saturation so that the introduction and removal of the dark bar produces a substantial modulation of the total surround input. The modulation is greater for the longer delay. At a relatively high cycle frequency (4 Hz, 4th row), the input sensitivity has insufficient time to recover and neither the bar onset of offset produces a non-negligible modulation. Bottom row: stimulus protocol.

Fig. 11. Responses of the model color-opponent neuron to a BT-like stimulus lacking sharp temporal boundaries. Left Column: Responses to a modified BT-like stimulus, in which the square-wave light-dark half-cycle was replaced with a pure sinusoidal modulation at the same fundamental frequency and the dark bar was replaced with a Gaussian temporal modulation of the same mean width. a_1-e_1) Same organization as a_1-e_1 in figure 8. A net response to the modified BT-like stimulus was clearly evident. Right Column: Responses to sinusoidal modulation of a large white spot. a_2-e_2) Same organization as a_1-e_1. Sinusoidal modulation alone evoked no net response.

Fig. 12. Effect of varying key temporal parameters. The integrated output of the model color-opponent cell to a BT-like stimulus is plotted as a function of cycle frequency for several different delays (for further details, see caption of figure 9, panel b). Left Column: Effects of changing the time delay (t_d) between red and green opponent inputs. Top row: Increasing the delay between from 7 to 9 msecs increased the overall magnitude of the response did not qualitatively modify the overall dependence on cycle frequency or onset delay. Middle row: Standard model. Bottom row. Decreasing the

delay from 7 to 5 msec decreased the overall magnitude of the response, but again did not affect the basic behavior of the model. Right Column: Effects of changing the adaptation time (t_{adapt}). Top row: t_{adapt} = 75 msec. Middle row: t_{adapt} = 50 msec (standard value). Bottom row: t_{adapt} = 25 msec. Smaller values of t_{adapt} reduced the responses to longer onset delays (blue traces) but did not otherwise affect the qualitative behavior of the model.

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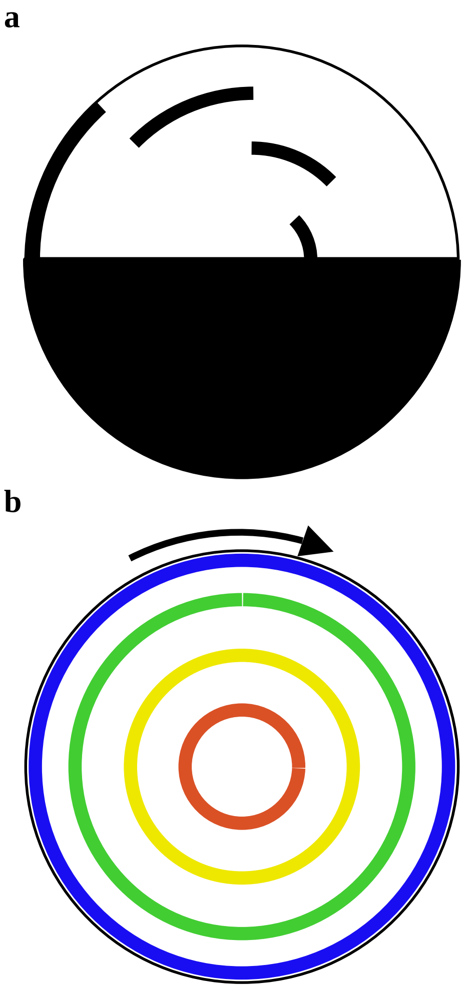


Fig 1

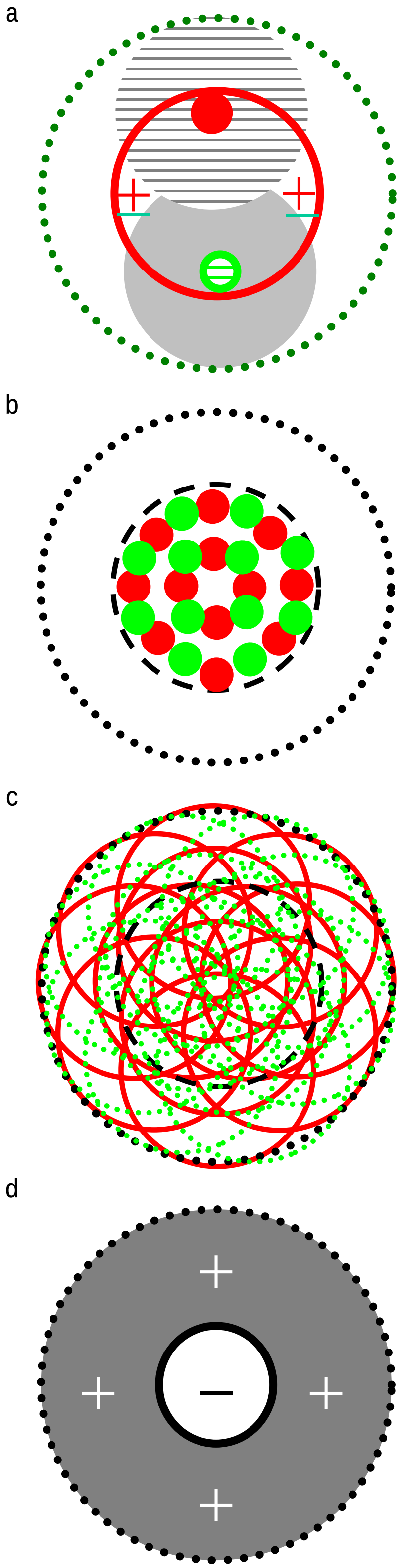


Fig 2

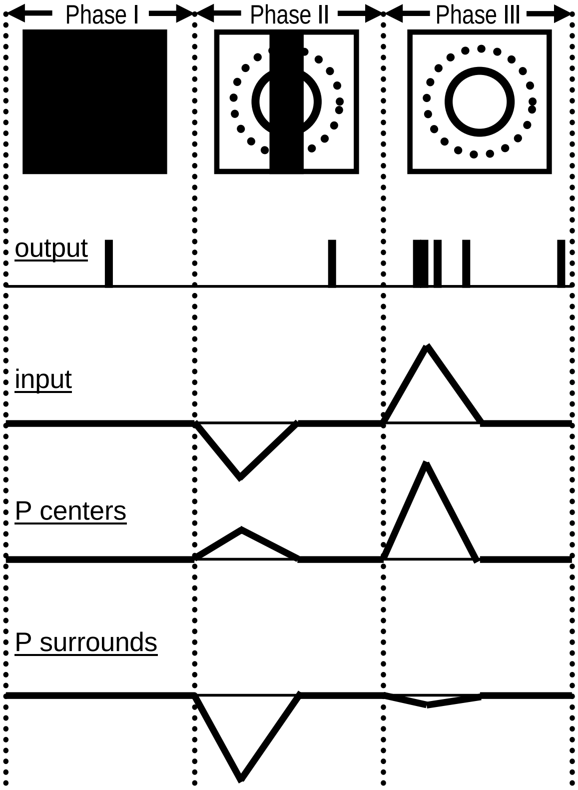

Phase I
Phase II
Phase III
output
input
P centers
P surrounds

Fig 3

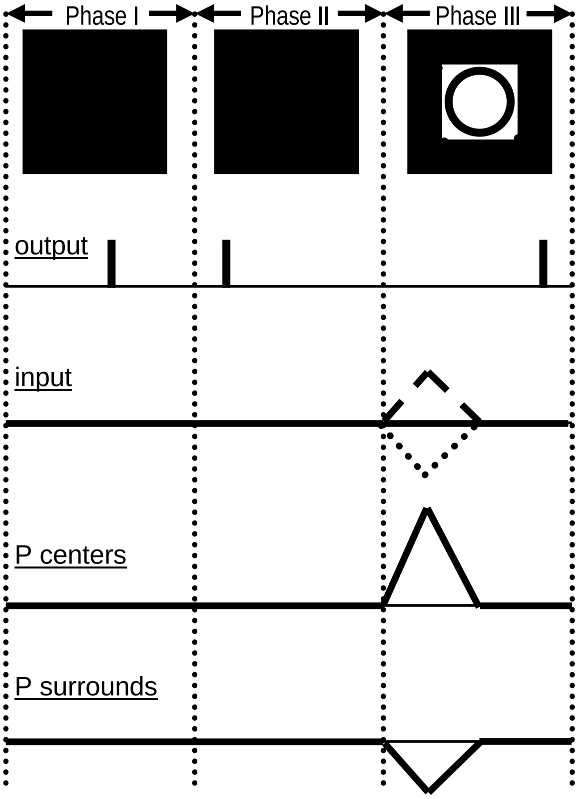
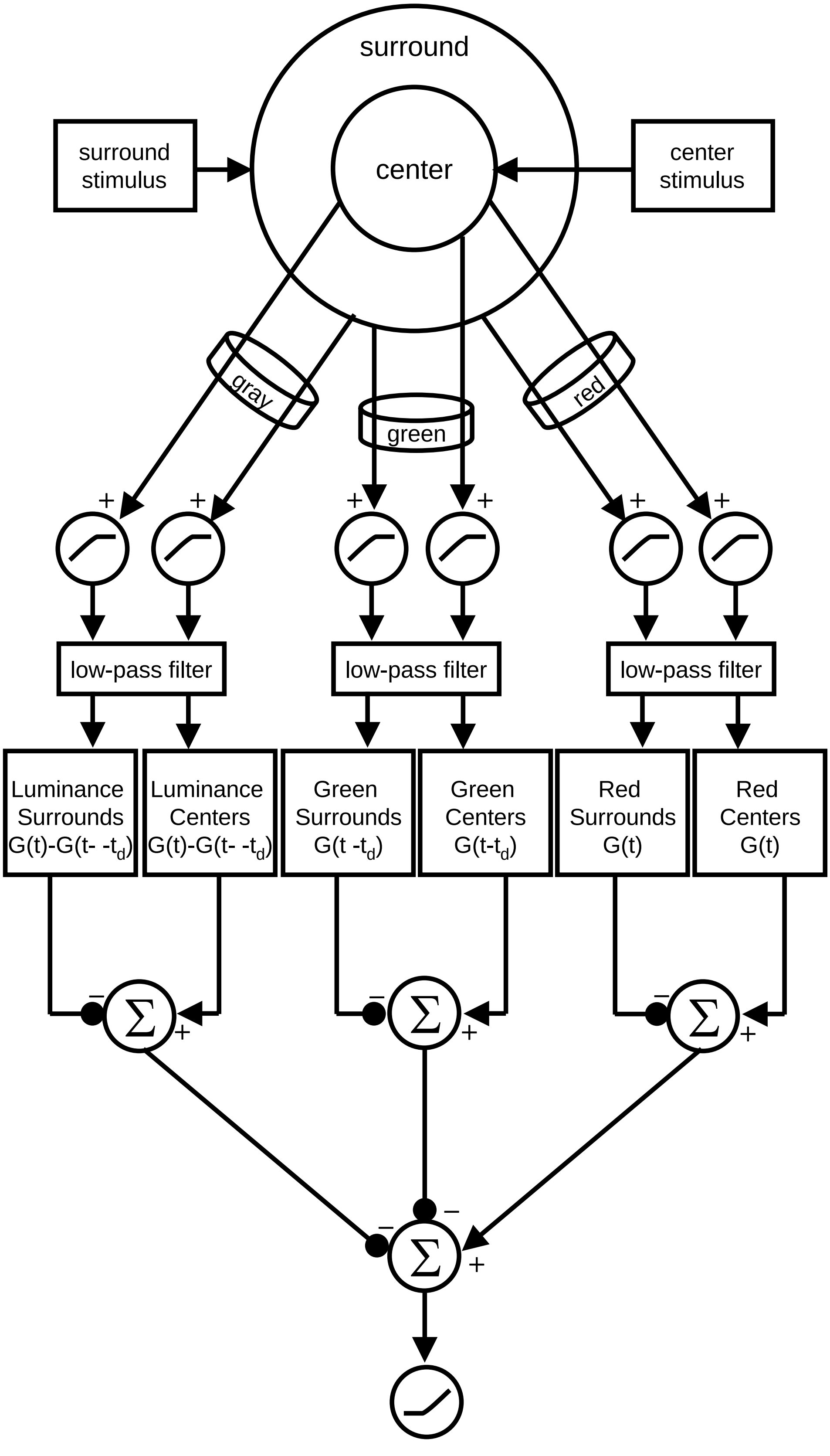

Phase I
Phase II
Phase III
output
input
P centers
P surrounds

Fig 4


surround
surround stimulus
center
center stimulus
gray
green
red
+
low-pass filter
low-pass filter
low-pass filter
Luminance Surrounds $G(t)-G(t- -t_d)$
Luminance Centers $G(t)-G(t- -t_d)$
Green Surrounds $G(t -t_d)$
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−
+
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Fig 5

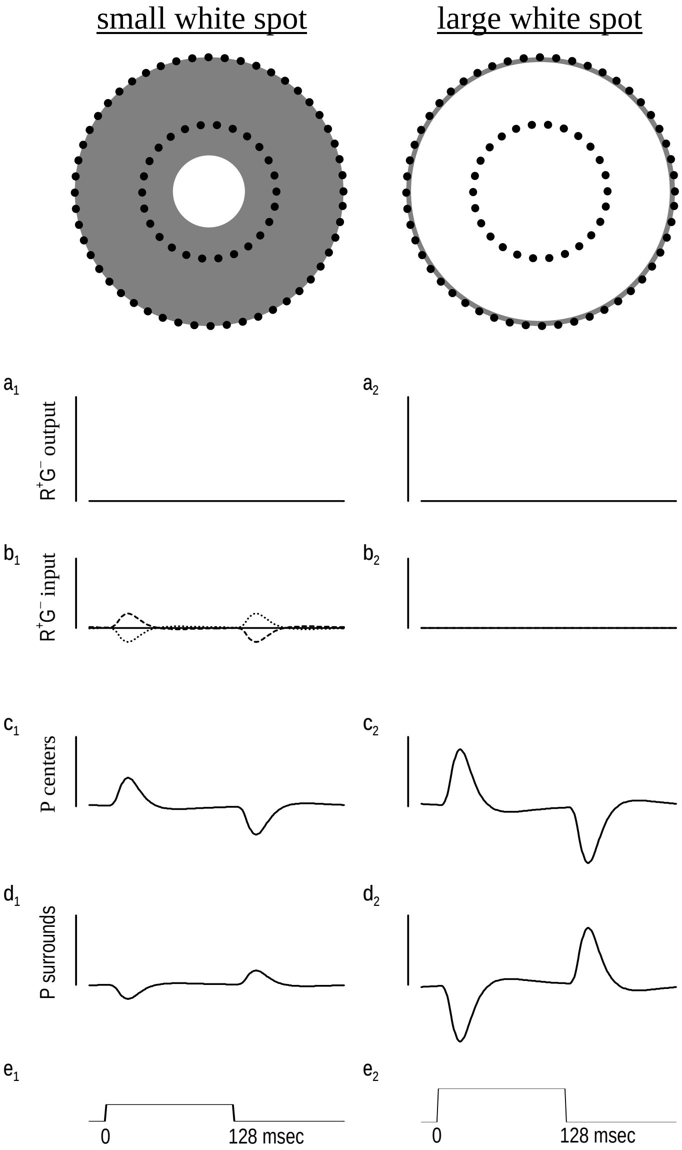
small white spot
large white spot
a1
a2
R+G− output
b1
b2
R+G− input
c1
c2
P centers
d1
d2
P surrounds
e1
e2
0
128 msec
0
128 msec

Fig 6

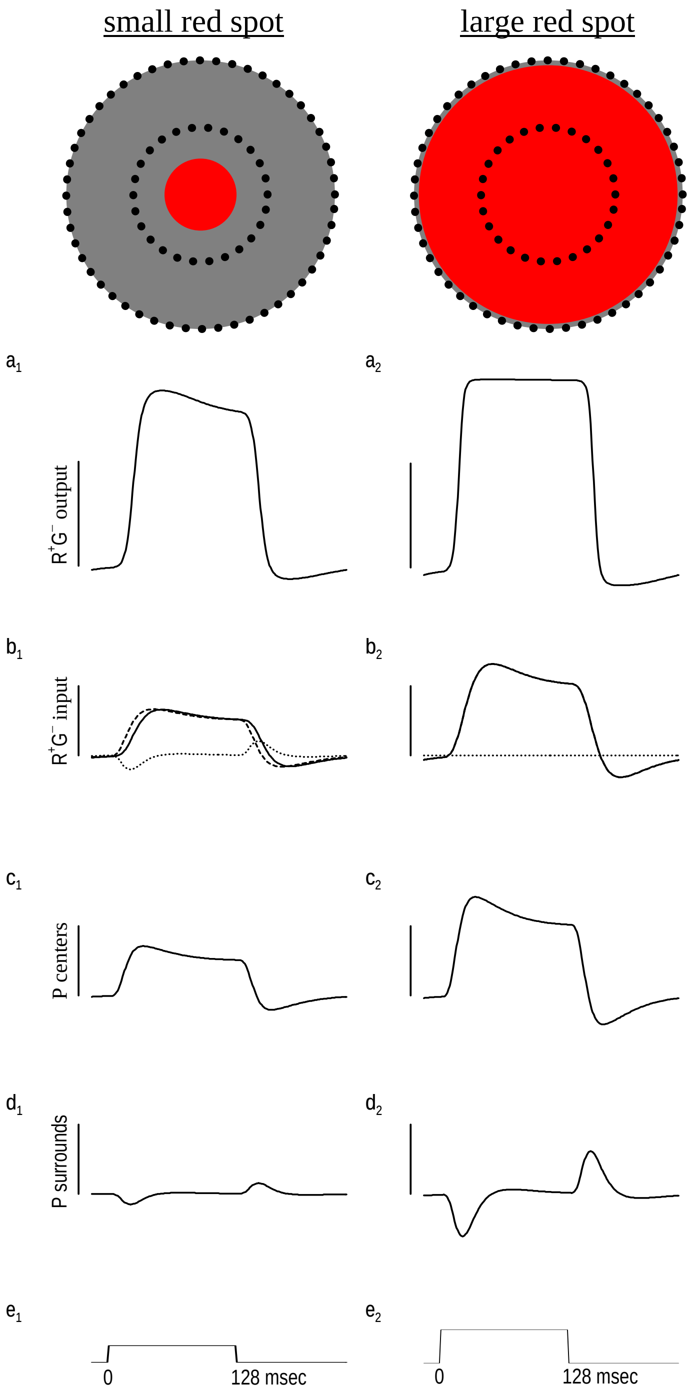
small red spot
large red spot
a1
a2
R+G− output
b1
b2
R+G− input
c1
c2
P centers
d1
d2
P surrounds
e1
e2
0
128 msec
0
128 msec

Fig 7

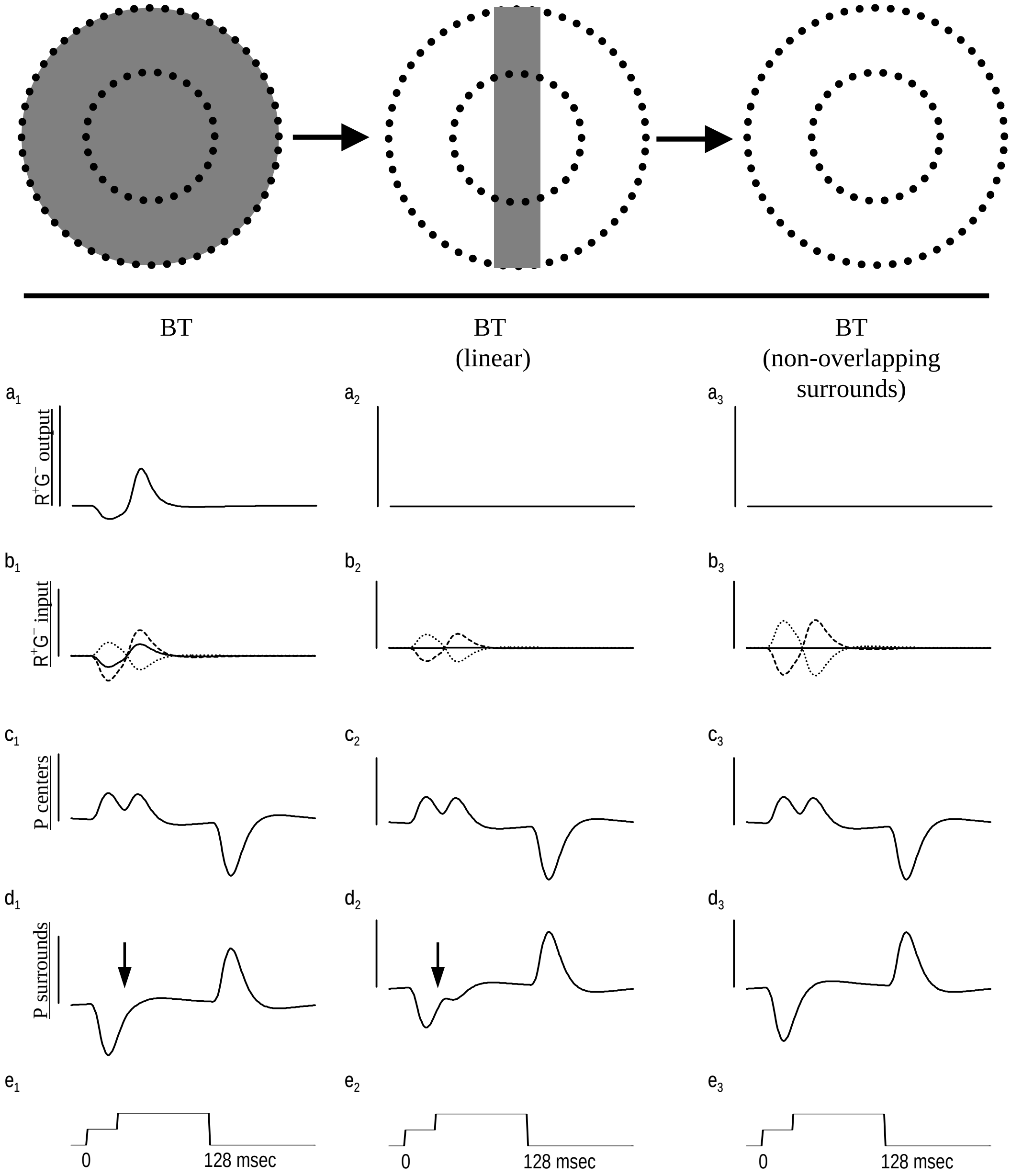
BT
BT
(linear)
BT
(non-overlapping
surrounds)
a1
a2
a3
R+G− output
b1
b2
b3
R+G− input
c1
c2
c3
P centers
d1
d2
d3
P surrounds
e1
e2
e3
0
128 msec
0
128 msec
0
128 msec

Fig 8

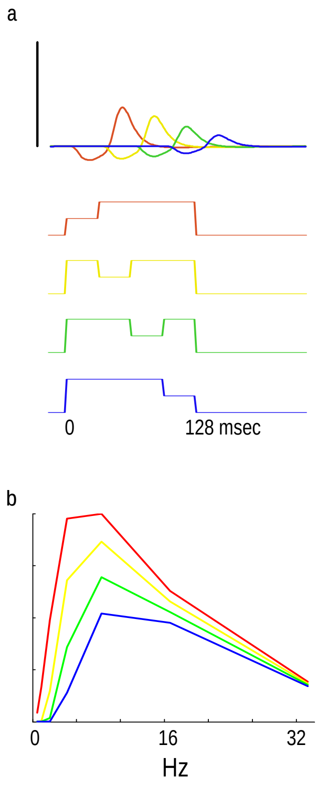

Fig 9

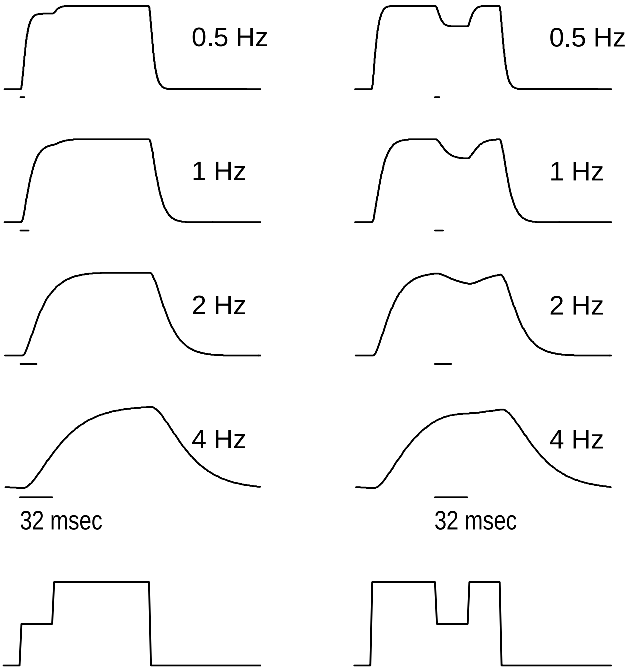

Fig 10

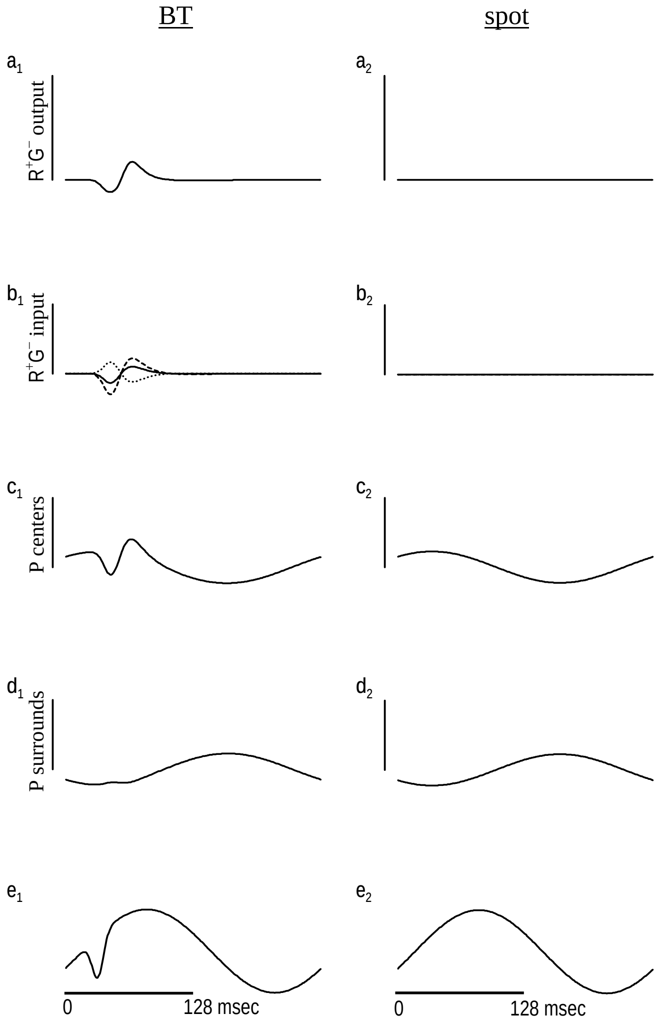
BT
spot
a1
a2
R+G− output
b1
b2
R+G− input
c1
c2
P centers
d1
d2
P surrounds
e1
e2
0
128 msec
0
128 msec

Fig 11

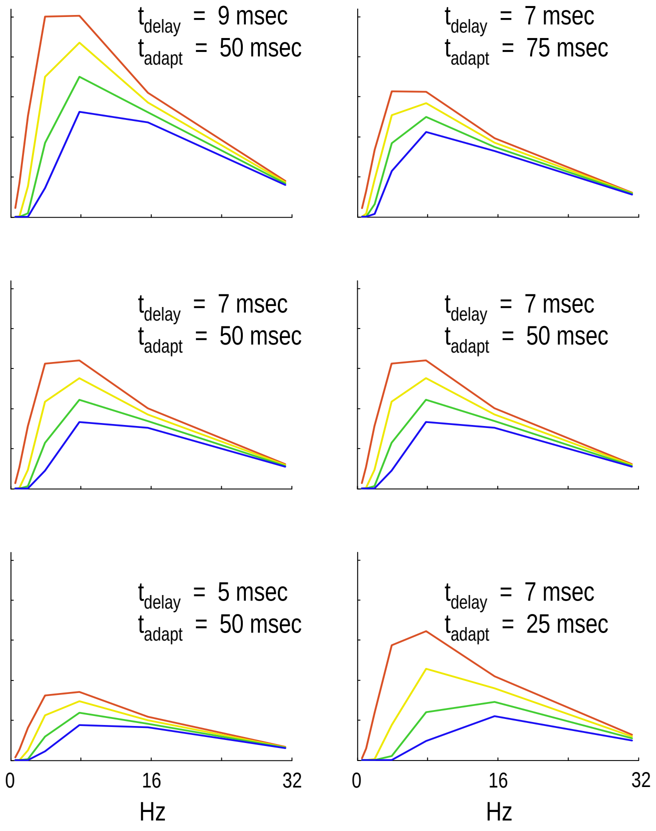
t_{delay} = 9 msec
t_{adapt} = 50 msec
t_{delay} = 7 msec
t_{adapt} = 75 msec
t_{delay} = 7 msec
t_{adapt} = 50 msec
t_{delay} = 7 msec
t_{adapt} = 50 msec
t_{delay} = 5 msec
t_{adapt} = 50 msec
t_{delay} = 7 msec
t_{adapt} = 25 msec
0
16
32
Hz
0
16
32
Hz

Fig 12